THE INFLUENCE OF HABITAT VARIABLES ON MARSH BIRD COMMUNITIES OF THE CONNECTICUT RIVER ESTUARY

Robert J. Craig[1] and Kathleen G. Beal[2]

Abstract.—Between 1974 and 1987, we studied summering birds of estuarine marshes along the Connecticut River in Connecticut in order to seek generalizations concerning the principal habitat features associated with species richness and species composition. Features of habitats investigated were (1) area, (2) environmental heterogeneity, (3) isolation, (4) water cover, (5) mudflat cover and, indirectly, (6) tidal and water salinity regimes. We also explored the value of large vs several small habitats in preserving marsh bird communities. Species inhabiting the marshes were divided into breeders (species that nested in marshes) and users (species that used marshes or associated creeks and flats primarily for feeding). Breeder species richness showed a significant positive relationship to marsh area and showed a negative relationship to water cover and environmental heterogeneity. User richness, in contrast, was positively related to proximity of additional marsh habitat (a measure of isolation), water cover, and environmental heterogeneity. Clustering pairwise comparisons of marshes showed that saline, strongly tidal marshes differed from freshwater, weakly tidal marshes. However, species composition was likely a consequence of the entire suite of differences which distinguish saline and freshwater marshes. Separately analyzing data on regularly occurring species, as opposed to all species recorded during the study period, produced similar results. Hence, the longer term view gained by considering all potentially occurring species yielded little additional information about habitat factors influencing species richness. In contrast, separately analyzing data on breeders and users demonstrated that these species groups had divergent principal habitat requirements. Series of small marshes proved to be equivalent or superior to a large marsh in supporting species richness. However, species occurring infrequently along the Connecticut River predominated at large marshes. *Received 5 June 1989, accepted 26 Nov. 1991.*

Evaluating the influence of habitat variables on bird species has been important for understanding patterns of avian community structure (Terborgh 1971, 1985; Anderson and Shugart 1974) and, consequently, for avian community management (Kantrud and Stewart 1984, Wiens and Rotenberry 1985). However, dissecting community-habitat relationships among the diverse avifaunas of structurally complex systems like three-dimensional forests may be difficult. Herbaceous marshes, although still complex, are essentially two-dimensional environments that support relatively few bird species. In ecological investigations, this relative simplicity is advantageous because the role of habitat variables in influencing

[1] Dept. Natural Resources Management and Engineering, U-87, Univ. Connecticut, Storrs, Connecticut 06269-4087. Present address: Northern Marianas College, P.O. Box 1250, Commonwealth No. Mariana Islands, Saipan, MP 96950.
[2] Dept. Mathematics and Statistics, Wright State Univ., Dayton, Ohio 45435.

community parameters may be less difficult to identify. We therefore studied birds of estuarine marshes along the Connecticut River in Connecticut in order to seek generalizations concerning avian community-habitat relationships. We wished to determine the principal habitat features associated with species richness and species distribution along the estuary. Furthermore, we investigated specific habitat features of estuarine wetlands likely to affect birds of these systems.

Habitat factors known to influence bird species richness and distributions in marshes are similar to those influencing terrestrial communities and include (1) tract size (Brown and Dinsmore 1986), (2) habitat diversity (Weller and Spatcher 1965, Weller and Fredrickson 1973, Kantrud and Stewart 1984), (3) isolation (Brown and Dinsmore 1986), and (4) history, including human impacts (Cottam and Bourne 1952, Clarke et al. 1984). Other habitat-related factors that affect marsh birds include water cover (Weller and Spatcher 1965), water level (Jackson 1983), tides (Burger 1985, Swift, 1988), and water salinity (Poulson 1969). We chose to study the relationship of marsh bird populations to (1) area, (2) environmental heterogeneity, (3) isolation, (4) water cover, (5) mudflat cover, and indirectly, (6) tidal and water salinity regimes. Historic changes in this system's avifauna are also reviewed.

Because marshes often exist as islands of discrete habitat, their bird communities have been studied in light of island biogeographic theory (e.g., Brown and Dinsmore 1986). Using predictions generated by this theory, investigators (e.g., Brown 1971, Butcher et al. 1981) have attempted to infer optimal designs for wildlife refuges. However, widely divergent viewpoints on the value of single large vs series of small refuges have been promoted (Simberloff and Abele 1976, Cole 1981). Furthermore, continental bird communities potentially differ from oceanic islands in the importance of such phenomena as colonization, extinction, and species use of surrounding habitats (Blake 1983). In temperate marshes, most residents are long-distance migrants with high dispersal ability. Moreover, the surrounding uplands can be used by many marsh species, whereas the open ocean is unsuitable habitat for terrestrial birds. With these considerations in mind, we explore the value of a large vs several small habitats in preserving marsh bird communities.

Earlier investigations of birds of the Connecticut River include Clark (1897), who described the nest of the Black Rail (*Laterallus jamaicensis*), Billard (1948), who estimated population densities of rails in freshwater marshes, and Poulson (1969), who studied the physiology of the Seaside (*Ammodramus maritima*) and Sharp-tailed sparrows (*A. caudacuta*). Several workers (e.g., Spitzer and Poole 1980) have studied population declines in nesting Ospreys (*Pandion haliaetus*) brought about by pollution of the river with toxic chemicals.

TABLE 1
SUMMARY OF HABITAT FEATURES OF THE CONNECTICUT RIVER MARSHES

Site	Type	Tides	Water salinity	Distance from river mouth (km)
Great Island (GI)[a]	salt marsh	yes	high	0.1
Black Hall River (BH)	salt marsh	yes	high	0.8
Upper Island (UI)	transitional	yes	moderate	1.3
Ragged Rock Creek (RR)	transitional	yes	moderate	2.6
Ayer's Point (AP)	brackish	yes	low	5.4
Lord's Cove (LC)	brackish	yes	low	6.0
Whalebone Creek (WC)	freshwater	yes	none	17.5
Pecausett Meadows (PM)	freshwater	yes	none	40.0
Cromwell Meadows (CM)	freshwater	yes	none	42.5
Dead Man's Swamp (DM)	freshwater	no	none	45.0
Wethersfield Meadows (WE)	freshwater	no	none	52.0

[a] Abbreviations of marsh names used in subsequent tables in parentheses.

STUDY AREAS AND METHODS

Study areas.—The Connecticut River estuary is bordered by a series of marshes totaling about 1200 ha. The 11 marshes studied intensively range from tidal salt marshes near the river mouth to nontidal freshwater marshes 52 km upriver (Table 1). Tidal amplitude, which during low river flows averages 1.1 m at the river mouth, declines to 0.5 m 60 km north at Hartford (NOAA 1983). Maximum water salinity varies from 17 ppt near the river mouth to 0 ppt 23 km upriver (Meade 1966).

A vegetation gradient is related to gradients in tidal amplitude and salinity. Five principal associations occur that are each structurally distinct because the diversity of dominant species is low. Around the river mouth are (1) shortgrass salt meadows composed largely of *Spartina patens, Distichlis spicata,* and *Juncus gerardi,* only occasionally inundated by tides (high salt marsh), and (2) rank intertidal cordgrass marshes of *Spartina alterniflora* and *Scirpus robustus* (low salt marsh). At about 2.6 km upriver, salt meadows are invaded by (3) strong-stemmed cattail-reed (*Typha angustifolia, Phragmites australis,* respectively) patches, which by 6.5 km upriver almost completely dominate the marshes. By 14 km upriver, freshwater communities occur, particularly (4) relatively soft-stemmed bulrush-tuckahoe-horsetail (*Scirpus fluviatilis, Peltandra virginica, Equisetum fluviatile,* respectively) marshes, and (5) floating-leaved pickerelweed-bullhead lily (*Pontederia cordata, Nuphar variegatum,* respectively) associations.

Habitat measurements.—Principal study sites (Table 1) included replicates of each of the four principal marsh types of the estuary: (1) salt marshes, containing predominantly high and low salt marsh; (2) transitional marshes, containing high and low salt marsh and cattail-reed habitats; (3) brackish cattail marshes, containing cattail-reed and low salt marsh; and (4) freshwater marshes, containing softstem bulrush and floating-leaved habitats. To assess further the effects of habitat size on species composition, we also studied separately the five freshwater marshes, including a large marsh and four relatively isolated, vegetationally similar small ones with a combined area similar to that of the large marsh.

We mapped vegetation types at each marsh on base maps made from 1:2400 aerial photographic enlargements. Marsh images from 1:12,000 1981 color infrared transparencies were superimposed on the enlargements with a Bausch and Lomb Zoom Transfer-scope.

Vegetation boundaries were then determined through photointerpretation (Civco et al. 1986). To check precision, maps were also field-checked for ground truth. We determined the area of each marsh and its component habitats by measuring the base maps with a compensating polar planimeter. Similar maps, based primarily on photointerpretation, were made for six of the largest marshes on 1:2400 1968 black-and-white photographic enlargements in order to assess the extent of vegetation change during the study period. Habitat patches covering <0.25 ha were too small to measure.

The area of water cover was determined on these same maps by measuring open water within the perimeter of each marsh. Although this was an imperfect measure because some marshes were bordered by the river while others were bordered by upland, we believe proximity to the river might be considered a constant because all sites were within 150 m of the main river channel. The extent of mudflats exposed at low tide was determined on the maps by measuring the mudflats within 100 m of the perimeter of each marsh. To determine the proximity of other marsh habitats, a measure of isolation, the distribution of all marshes of the Connecticut River was traced on acetate cellulose laid over 1:12,000 black-and-white photographs. The area of other marshes present within 1 km of the perimeter of each study site was then measured. Although the distances to which we measured mudflats and other marshes were arbitrarily chosen, this procedure included most mudflats and other marshes near the study sites. Finally, the area of each marsh was computed in two ways, considering (1) only vegetated areas (marsh area) and (2) vegetated areas, mudflats and water cover (total area).

Bird surveys. — Marsh bird distributions were studied by Craig from 1974 to 1987. Data on summering birds were gathered between early May and mid-July, but observations that shed additional light on breeding status were made at all seasons. Depending on the size of the marsh, 5–10 h per day were typically spent surveying, but shorter visits were made when checking for the presence of individual species. Observations usually began at dawn, and all sites were also visited from afternoon to dusk. Most sites also were visited after dark. Birds were observed for 1073 h, including 29–81 h of summer observations at each of the 11 principal study areas.

While crossing a marsh on foot or by boat during a visit, we recorded all bird species encountered. Data from all visits were used to prepare lists of summering species for each site. Based on our data and those of collaborating observers, species were divided into those that were (1) regular — occurring at a site most years, and (2) occasional — occurring irregularly, generally <50% of breeding seasons. This distinction permitted comparisons of habitat variables with the typical assemblage of birds (regular species) and with the entire potential assemblage of birds (regular + occasional species) that found suitable habitat conditions along the estuary. The latter comparison allowed for exploration of habitat relationships in the absence of such factors as externally driven population phenomena.

Summering species were classified into two additional groups: (1) breeders — species that spent their entire day on marshes, nesting there, and using marsh vegetation, creeks, or tidal flats, and (2) users — species that used marshes or associated creeks and flats primarily for feeding but which nested elsewhere. This distinction permitted separate analysis of habitat variables with species closely tied to marsh environments for all aspects of their survival and of species that opportunistically exploited marshes for food resources that were in many cases indefensible (e.g., schooling fish).

In most cases, breeding evidence was confirmed (nests, eggs, nestlings, fledglings, family groups) for those species termed breeders. However, we classified summering individuals of several species as breeders because in their habitat use they best conformed to this definition. For example, the few nonbreeding Northern Harriers (*Circus cyaneus*) present appeared to feed exclusively in marshes and at least attempted breeding. Similarly, Wood

Ducks (*Aix sponsa*) were called breeders because they spent essentially all their time in marshes even though they nested in tree holes or boxes adjacent to the marshes. We did not include postbreeding flocks (e.g., swallows, herons), migrants, or summer vagrant species in this study but focused solely on birds of the breeding season.

Analysis.—Shannon and Weaver's (1963) formula was used to compute indices of habitat diversity, H′ from the proportion of each habitat in a marsh. We made separate computations for marsh vegetation types (vegetation heterogeneity) and for vegetation, water, and mudflats considered together (habitat heterogeneity).

To compute habitat similarity between pairs of marshes we developed an index of similarity (IS) based on that of Spatz (Mueller-Dombois and Ellenberg 1974):

$$IS = \sum d_i n^{-1} / \sum (p_i + q_i) tot^{-1}$$

where d_i is the proportion of habitat i at a marsh divided by the larger proportion at the compared marsh, n is the total number of habitats at the two marshes, p_i and q_i are the areas of the shared habitat i at the compared marshes, and tot is the total area of all habitats at the compared sites. The numerator weights the index for the number of habitats and the denominator weights for proportionate similarity in cover. We used this formula to determine vegetation similarity and similarity of all habitats (habitat similarity).

To compute differences in marsh area, mudflat area, and marsh proximity, we developed the index of difference (ID): $ID = |a_i - a_j| / (a_i + a_j)$, where a is the area of cover at the compared marshes i and j. Similarity in species composition was assessed by dividing the number of shared species by the total species pool at the compared marshes.

Using diagnostics described by Myers (1986) and SAS (1985) Proc Reg procedures, we evaluated collinearity among the seven habitat regressor variables. We then analyzed species richness vs regressor variables from each set of independent variables to determine the best fitting statistical models. In making decisions concerning best fit, we considered the significance of the parameter estimates, r^2 (the coefficient of determination), collinearity diagnostics (correlations of estimates, variance inflation factors, eigenvalues, condition numbers, variance proportions), and residual plots. Normality assumptions were assessed with normal probability plots of residuals generated using the final regression model.

Relationships among marshes in their species and habitat similarities were explored with cluster analysis, a descriptive statistical technique (Morrison 1990) and SAS (1985) Proc Cluster procedures. Three clustering methods were performed: average linkage, complete linkage, and centroid hierarchical, with cluster number determined by the computer. Cluster analysis was chosen because similarity data were not independent, and conventional hypothesis testing was, therefore, not valid.

RESULTS

Habitat-species richness relationships.—Marsh area, total area, marsh proximity and mudflat cover (Table 2) all tended to increase toward the river mouth, and five measures of collinearity showed them to be highly related. Hence, they constituted a set of variables, one of which was included in each multiple regression model investigated. Although direct measurements were not made on tidal and salinity patterns, they appeared to correlate positively with these measures. Vegetation and habitat heterogeneity (Table 2) were also highly related to each other, although not to other habitat measures. They constituted another set of variables, one

TABLE 2
MEASUREMENTS OF HABITAT FEATURES AT 11 CONNECTICUT RIVER MARSHES

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
Heterogeneity											
Marsh	0.77	0.70	0.59	0.84	0.23	0.24	0.74	0.33	0.31	0.38	0.39
Habitat	0.97	1.22	1.11	1.11	0.63	0.78	1.30	0.91	0.84	0.42	0.42
Area (ha)											
Marsh	145.6	56.4	121.6	155.4	39.5	215.2	23.1	21.6	119.7	26.9	30.7
Habitat	153.4	74.7	155.2	169.5	44.9	274.3	31.6	30.3	146.6	27.1	30.9
Mudflats (ha)	3.6	13.6	24.1	6.7	1.1	6.6	3.1	0.6	7.4	0	0
Water (ha)	4.2	4.7	9.5	7.5	4.4	52.4	5.5	8.1	19.7	0.2	0.2
Proximity (ha)	131.0	161.3	188.2	49.5	31.0	76.6	5.6	10.4	6.4	1.2	12.9

of which was included in each multiple regression model tested. Water cover (Table 2) was independent of all other habitat measures and was, therefore, entered into all multiple regression models.

In comparing species richness to habitat variables, the model best fitting both all (Fig. 1a) and regular (Fig. 1b) breeders contained total area, water cover, and habitat heterogeneity (see Craig 1990 for a complete listing of species occurrence). All breeder richness was inversely related to water cover and habitat heterogeneity and directly related to total area. All three habitat measures made a significant contribution to the model ($r^2 = 0.94$; total area $t = 9.93$, $P < 0.0001$; water cover $t = -6.58$, $P < 0.0003$; habitat heterogeneity $t = -2.43$, $P < 0.05$; 7 df). Replacing habitat heterogeneity with vegetation heterogeneity only slightly reduced the fit of the model.

The relationship of regular breeder richness to water cover and total area was similar to that of all breeders, but the partial slope for habitat heterogeneity was not significant in the presence of the other two habitat measures ($r^2 = 0.87$; total area $t = 6.45$, $P < 0.0004$; water cover $t = -5.15$, $P < 0.0001$; habitat heterogeneity $t = -0.39$, $P < 0.70$; 7 df). Replacing total area with marsh area and/or habitat heterogeneity with vegetation heterogeneity only slightly reduced the fit of the model.

For both all (Fig. 2a) and regular (Fig. 2b) users, marsh proximity, water cover, and vegetation heterogeneity produced the best fitting regression model, although replacing vegetation with habitat heterogeneity did not greatly affect results. All independent variables were positively related to species richness (all users $r^2 = 0.87$; marsh proximity $t = 3.79$, $P < 0.007$; water cover $t = 2.97$, $P < 0.02$; vegetation heterogeneity $t = 2.57$, $P < 0.04$; 7 df; regular users $r^2 = 0.85$; marsh proximity $t = 3.73$, $P < 0.007$; water cover $t = 2.45$, $P < 0.04$; vegetation heterogeneity $t = 2.16$, $P < 0.07$; 7 df).

Analysis of changes in vegetative cover at six sites between 1968 and 1981 indicated that most marsh types had stable vegetation patterns. Black Hall River, Great Island, Lord's Cove, and Cromwell Meadows underwent little vegetational change. Wethersfield Meadows showed a small increase in cattail cover, but the extent of high and low salt marsh dropped at Upper Island. Expansion and contraction of vegetation zones in Long Island Sound tidal marshes has been related to long term lunar cycles (Civco et al. 1986). The only consequence of this habitat shift detected during the study period was that populations of Seaside and Sharp-tailed sparrows were reduced, although not eliminated, at transitional marshes (Craig 1990).

Pairwise marsh comparisons. — All three procedures used in cluster analysis on pairwise comparative data (Tables 3, 4) yielded similar groupings
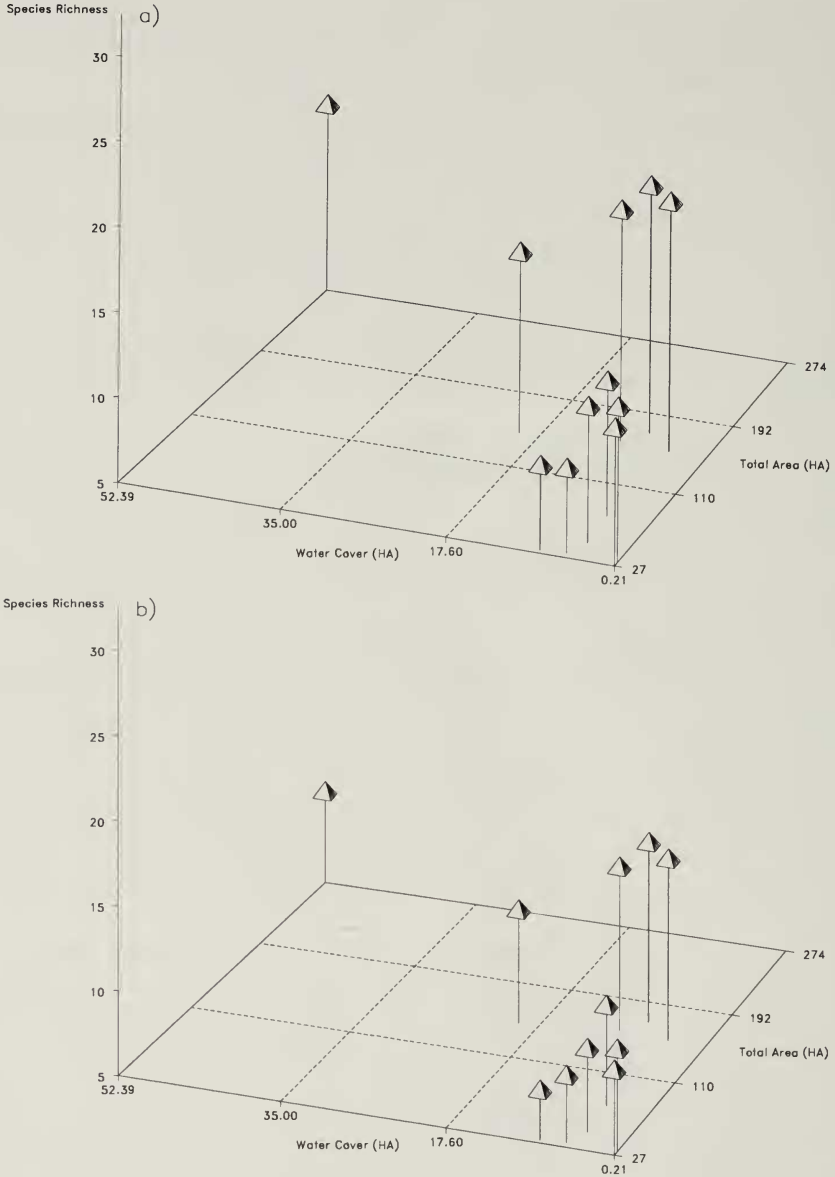
FIG. 1.   The relationship between breeder richness, total area, and water cover for (a) all breeders, and (b) regular breeders.
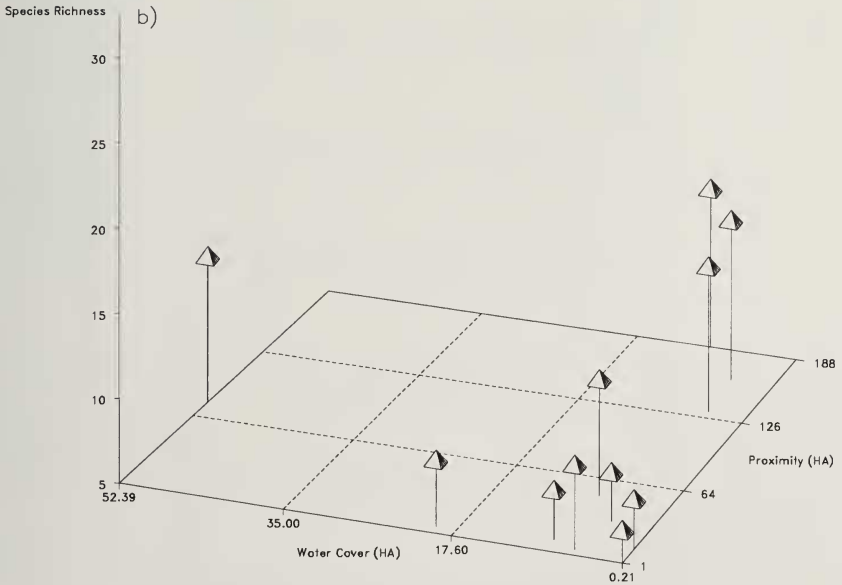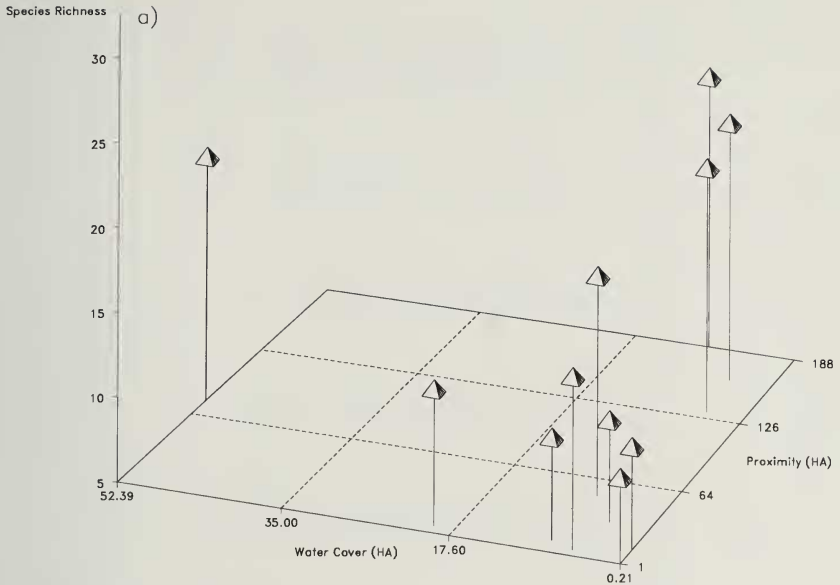
FIG. 2.   The relationship between user richness, marsh proximity, and water cover for (a) all users, and (b) regular users.

TABLE 3
PERCENT SIMILARITY IN BREEDER SPECIES COMPOSITION

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
GI	—	54.5[a]	56.4	78.3	54.5	69.6	39.1	43.5	52.0	44.0	52.2
BH	68.8	—	63.2	63.2	41.2	38.1	37.5	35.3	33.3	30.0	31.6
UI	88.2	68.8	—	90.0	63.2	71.4	45.0	42.9	52.2	37.5	45.5
RR	77.8	58.8	88.2	—	63.2	63.6	45.0	42.9	59.1	43.5	45.5
AP	47.1	42.9	47.1	56.3	—	70.6	69.2	64.3	64.7	52.9	66.7
LC	55.6	43.8	55.6	64.7	75.0	—	50.0	55.6	65.0	47.6	57.9
WC	47.1	42.9	47.1	47.1	50.0	61.5	—	61.5	52.9	50.0	64.3
PM	47.1	33.3	47.1	47.1	63.6	50.0	63.6	—	68.8	66.7	84.6
CM	52.9	40.0	52.9	52.9	72.7	57.1	58.3	90.0	—	66.7	70.6
DM	47.4	35.3	47.4	47.4	61.5	60.0	61.5	61.5	69.2	—	80.0
WE	44.4	23.5	44.4	44.4	46.2	46.7	58.3	72.7	66.7	69.2	—

[a] Above diagonal = all breeders, below diagonal = regular breeders.

TABLE 4
PERCENT SIMILARITY IN USER SPECIES COMPOSITION

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
GI	—	86.4[a]	86.4	90.5	65.0	85.7	57.1	65.0	70.0	40.0	40.0
BH	76.5	—	82.6	95.2	61.9	81.8	47.8	54.5	59.1	38.1	31.8
UI	70.6	61.1	—	86.4	61.9	81.8	61.9	61.9	59.1	38.1	38.1
RR	75.0	75.0	80.0	—	65.0	77.3	50.0	57.1	61.9	40.0	33.3
AP	41.2	60.0	53.3	57.1	—	68.4	73.3	73.3	68.8	61.5	50.0
LC	55.6	64.7	80.0	73.3	69.2	—	60.0	68.4	65.0	42.1	42.1
WC	33.3	41.2	43.8	37.5	63.6	46.7	—	73.3	68.8	61.5	61.5
PM	38.9	47.1	60.0	53.3	72.7	76.9	58.3	—	92.9	61.5	61.5
CM	38.9	47.1	60.0	53.3	72.7	76.9	58.3	100	—	57.1	57.1
DM	31.3	31.3	33.3	35.7	50.0	46.2	50.0	60.0	60.0	—	77.8
WE	23.5	40.0	33.3	35.7	66.7	46.2	66.7	60.0	60.0	71.4	—

[a] Above diagonal = all users, below diagonal = regular users.

TABLE 5

CLUSTERS OF PAIRWISE COMPARISONS BETWEEN MARSHES

Site	GI	BH	UI	RR	AP	LC	WC	PM	CM	DM	WE
GI	—	3[a]	4	4	1	2	1	1	1	1	1
BH		—	4	4	1	1	1	1	1	1	1
UI			—	3	3	3	1	1	1	1	1
RR				—	3	4	1	1	1	1	1
AP					—	5	2	2	2	1	2
LC						—	1	2	2	1	1
WC							—	3	3	2	2
PM								—	6	2	2
CM									—	2	2
DM										—	3

[a] Numbers refer to membership in clusters 1–6.

of marshes. Results of average linkage cluster analysis are summarized here. For six clusters (Table 5), the largest cluster (27 members) was principally composed of pairwise comparisons between strongly saline, highly tidal influenced (salt, transitional) marshes and freshwater, low tidal influenced marshes. To a lesser extent, saline and brackish cattail marshes were compared. Differences between saline and freshwater marshes principally resulted from the disappearance of certain waterfowl, Clapper (*Rallus longirostris*) and King rails (*R. elegans*), Willets (*Catoptrophorus semipalmatus*), Ospreys, terns, Fish Crows (*Corvus ossifragus*), Seaside and Sharp-tailed sparrows, and several species of waders at freshwater marshes. American Bitterns (*Botaurus lentiginosus*), Soras (*Porzana carolina*), and Wood Ducks, which predominated at freshwater marshes, also contributed to the difference.

Cluster 2 (13 members) consisted primarily of marsh pairs with low salinity and low mudflat areas. Such areas have few waders, gulls, and terns. Cluster 3 (8 members) was predominantly comparisons of sites with similar vegetation and water cover. Cluster 4 (6 members) compared salt vs transitional marshes, and clusters 5 and 6 (1 member each) compared small vs large marshes.

Refuge design.—The number of combined species at the four small freshwater marshes, Whalebone Creek, Pecausett Meadows, Dead Man's Swamp and Wethersfield Meadows, was the same as at the large Cromwell Meadows for all breeders (16) and surpassed Cromwell Meadows for regular breeders (14 vs 10). The four marshes had more species of both all (15 vs 14) and regular (12 vs 10) users than did Cromwell Meadows. Only two breeders occurred no more than occasionally at the small marsh-

es, but six occasional breeders were at Cromwell Meadows. Small marshes had three species of occasional users, whereas Cromwell Meadows had four.

The sole breeders present only at Cromwell Meadows were the Canada Goose (*Branta canadensis*) and Blue-winged (*Anas discors*) and Green-winged teal (*A. crecca*), all occasional breeders there. However, Craig (1990) found Blue-winged Teal summering at the relatively small (25 ha) South Windsor Meadows, a Connecticut River marsh outside the principal study area. Of those breeders present only at small freshwater marshes, the Mute Swan (*Cygnus olor*) was observed only at Whalebone Creek, and the Pied-billed Grebe (*Podilymbus podiceps*) occurred once at Dead Man's Swamp. Among users, only the Glossy Ibis (*Plegadis falcinellus*) occurred solely at Cromwell Meadows, a single occurrence. Users limited to small marshes were the Osprey and Purple Martin (*Progne subis*) which were solely at Whalebone Creek.

DISCUSSION

The principal importance of area in predicting breeder species richness was consistent with findings from other studies of habitat islands (Howe 1984, Brown and Dinsmore 1986). Habitats, which can be more diverse in larger tracts, are thought to be responsible in part for the positive relationship (Rafe et al. 1985). However, in this study the effects of area were separated from those of habitat heterogeneity, which proved weakly or negatively related to species richness. Most breeding species used more than one habitat type (Craig 1990), and therefore increased heterogeneity did not translate into greater species number. Hence, area alone seemed an important determinant of breeder richness.

A species-area relationship may exist in part because the probability of migrant colonization is positively related to total area. Craig (1990), for example, reported that Connecticut River species existing at low densities, such as the Black Rail, King Rail, and Willet often inhabited large marshes. In addition, increased total area may be related to improved habitat quality, as can be the case with forest tracts (Blake 1987). Although Craig (1990) found that even wide-ranging species could occur at the smallest sites, several species of waterfowl and the Northern Harrier predominated at large marshes, suggesting that such sites were superior as habitats.

The negative relationship between water cover and breeder richness was largely a consequence of sites with very high water cover, like Lord's Cove and Cromwell Meadows, having fewer bird species than downriver sites with relatively little water cover. The species added at the downriver marshes (e.g., Clapper Rail, Willet, Seaside and Sharp-tailed sparrows)

are not generally associated with extensive open water. Furthermore, the river channel, present near all sites, may have provided sufficient open water for those species requiring it, thereby minimizing the importance of creeks and ponds present within marsh perimeters. Breeders that frequently feed in or at the edge of open water, such as bitterns and waterfowl, were not eliminated even from sites like Dead Man's Swamp, which had almost no open water. Although open water may benefit certain species (Weller and Spatcher 1965), beyond some threshold level apparently surpassed by all sites in this study, additional open water appears to have no value in increasing bird species richness.

Proximity to additional marsh habitat was important to user richness because certain species clustered around the river mouth where marsh proximity also tended to be greatest. More species, especially wide-ranging ones such as waders, gulls, and terns that must track indefensible, ephemeral prey sources (Krebs 1974) were apparently attracted to areas with more extensive foraging habitat. Traveling between sites may be more effective for foraging than remaining at a single site when searching for ephemeral prey, even when a marsh is large (see also Gibbs et al. 1987). The positive relationship between water cover and user richness further showed that, unlike breeders, users were attracted to areas with more open water in the form of marsh creeks and ponds. Such open water areas were prime foraging sites for species such as waders and terns.

The association of vegetation and habitat heterogeneity with user richness showed that unlike for breeders, the mosaic of habitats present was important to users. The value of such a heterogeneous landscape to users is clear: tidal flats and creeks provide foraging sites for the waders, gulls, terns, and swallows that make up most of the user species, whereas the marsh surface is used for resting and feeding.

Separately analyzing data on all and regular species produced similar results. Hence, the longer term view gained by considering all potentially occurring species yielded little additional information about habitat factors influencing species richness. In contrast, separately analyzing data on breeders and users demonstrated that these species groups have divergent principal habitat requirements. Based on partial regression residual plots (Myers 1986), breeder richness was most strongly influenced by total area and water cover, whereas user richness was most closely related to marsh proximity. Moreover, breeders and users responded inversely to the presence of water cover and environmental heterogeneity.

Clustering pairwise comparisons of marshes showed that saline, strongly tidal marshes strongly differed from freshwater, weakly tidal marshes. Similarity for breeders and users was 23–66%, among the lowest similarity figures computed. Such a distinction is expected in light of the physio-

logical (e.g., Poulson 1969) and behavioral (e.g., Jackson 1983, Burger 1985) adaptations that salt marsh species show for high salinity and tidal fluctuations. However, such factors as marsh proximity, mudflat cover, salinity, and tidal patterns are highly correlated, and therefore, species composition is likely a consequence of the entire suite of differences which distinguish saline and freshwater marshes. The secondary clusters of marsh pairs based on vegetation, water cover, and area suggest that these factors had an influence on species composition as well. Hence, marshes of the same size with similar habitat conditions should attract similar species of birds.

Refuge design.—Even though we demonstrated a species-area relationship for marsh breeders, our findings for the five freshwater marshes are inconsistent with Cole's (1981) theoretical prediction that systems inhabited by good colonizers (i.e., migrants) should have more species on a large habitat island than on several small ones. Combined, the small marshes had a number of breeder and user species equivalent to or greater than that of the large marsh even though each was relatively isolated. Furthermore, they had more regular breeders and users than Cromwell Meadows, which had more occasionally occurring species.

The presence of more occasionally occurring species at Cromwell Meadows may be understood in light of the species-area relationship uncovered for this system. Improved probability of migrant colonization and better habitat quality at large marshes may make species occurring at low densities more likely to colonize them. At least eight of the ten species that occurred occasionally at Cromwell Meadows, and all three of the species unique to this marsh, occurred infrequently in freshwater parts of the river (Craig 1990).

In conclusion, series of small marshes, within the range of sizes considered and within the context of present regional population levels, appeared effective in preserving the species richness of the Connecticut River system. However, they appeared to be less effective than larger marshes in supporting species that exist at low densities. Whether these small marshes can continue to sustain adequate populations to ensure species persistence in the absence of large marshes is as yet unknown.

LITERATURE CITED

ANDERSON, S. H. AND H. H. SHUGART. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828–837.

BILLARD, R. S. 1948. An ecological study of the Virginia Rail and the Sora in some Connecticut swamps, 1947. M.S. thesis, Iowa State Univ., Ames, Iowa.

BLAKE, J. G. 1983. Trophic structure of bird communities in forest patches in east-central Illinois. Wilson Bull. 95:416–430.

———. 1987. Species-area relationships of winter residents in isolated woodlots. Wilson Bull. 99:243–252.

BROWN, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. Am. Nat. 105:467–478.

BROWN, M. AND J. J. DINSMORE. 1986. Implications of marsh size and isolation for marsh bird management. J. Wildl. Manage. 50:392–397.

BURGER, J. 1985. Habitat selection in temperate marsh-nesting birds. Pp. 253–281 *in* Habitat selection in birds (M. L. Cody, ed.). Academic Press, New York, New York.

BUTCHER, G. S., W. A. NIERING, W. J. BARRY, AND R. H. GOODWIN. 1981. Equilibrium biogeography and the size of nature preserves: an avian study. Oecologica 49:29–37.

CIVCO, D. L., W. C. KENNARD, AND M. W. LEFOR. 1986. Changes in Connecticut salt marsh vegetation as revealed by historical aerial photographs and computer-assisted cartographics. Env. Manage. 10:229–239.

CLARK, J. H. 1897. The Little Black Rail. Auk 1:393–394.

CLARKE, J., B. A. HARRINGTON, T. HRUBY, AND F. E. WASSERMAN. 1984. The effects of ditching for mosquito control on salt marsh use by birds in Rowley, Massachusetts. J. Field Ornithol. 55:160–180.

COLE, B. J. 1981. Colonizing abilities, island size, and the number of species on archipelagoes. Am. Nat. 117:626–638.

COTTAM, C. AND W. S. BOURNE. 1952. Coastal marshes adversely affected by drainage and drought. Trans. N. Amer. Wildl. Conf. 17:414–420.

CRAIG, R. J. 1990. Historic trends in the distribution and populations of estuarine marsh birds of the Connecticut River. Univ. Conn., Storrs Agr. Expt. Sta. Res. Report 83.

GIBBS, J. P., S. WOODWARD, M. L. HUNTER, AND A. E. HUTCHINSON. 1987. Determinants of Great Blue Heron colony distribution in coastal Maine. Auk 104:38–47.

HOWE, R. W. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. Ecology 65:1585–1601.

JACKSON, J. A. 1983. Adaptive response of nesting Clapper Rails to unusually high water. Wilson Bull. 95:308–309.

KANTRUD, H. A. AND R. E. STEWART. 1984. Ecological distribution and crude density of breeding birds of prairie wetlands. J. Wildl. Manage. 48:426–437.

KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51:99–131.

MEADE, R. H. 1966. Salinity variations in the Connecticut River. Water Resour. Res. 2: 567–579.

MORRISON, D. F. 1990. Multivariate statistical methods. McGraw-Hill, New York, New York.

MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley, New York, New York.

MYERS, R. H. 1986. Classical and modern regression with applications. Duxbury Press, Boston, Massachusetts.

NOAA. 1983. Tide tables 1984; east coast of North and South America. U.S. Dept. Commerce, NOAA.

POULSON, T. C. 1969. Salt and water balance in Seaside and Sharp-tailed sparrows. Auk 86:473–489.

RAFE, R. W., M. B. USHER, AND R. G. JEFFERSON. 1985. Birds on reserves: the influence of area and habitat on species richness. J. Appl. Ecol. 22:327–336.

SAS INSTITUTE, INC. 1985. SAS user's guide: statistics, 5th ed. SAS Institute, Cary, North Carolina.

SHANNON, C. E. AND W. E. WEAVER. 1963. The mathematical theory of communication. Univ. Illinois Press, Urbana, Illinois.

SIMBERLOFF, D. S. AND L. G. ABELE. 1976. Island biogeography theory and conservation practice. Science 191:285–286.

SPITZER, P. R. AND A. POOLE. 1980. Coastal Ospreys between New York and Boston: a decade of reproductive recovery. Am. Birds 34:234–241.

SWIFT, B. L. 1988. Models of avian breeding habitats in Hudson River tidal marshes. N.Y. Dept. Env. Cons., Div. Fish and Wildl. Final Report.

TERBORGH, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52:23–40.

———. 1985. The role of ecotones in the distribution of Andean birds. Ecology 66:1237–1246.

WELLER, M. W. AND L. H. FREDRICKSON. 1973. Avian ecology of a managed glacial marsh. Living Bird 12:269–291.

——— AND C. E. SPATCHER. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa State Univ. Special Report 43.

WIENS, J. A. AND J. T. ROTENBERRY. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Ecology 22:655–668.